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I.—On the Metamorphoses of the Vorticellæ. By M. JULES D'UDEKEM*.

THE history of the development of the Infusoria has remained one of the most obscure questions in natural science.

The older authors, who had but very imperfect means of observation at their disposal, took little note of it, and this only with a view to one object—namely, to prove the existence of spontaneous generation. The inutility of their efforts is well known. Modern naturalists have observed the Infusoria rather under the point of view of zoology than of physiology; and it is really only within the last few years that the history of the development of the Infusoria has acquired a prominent place, and that observers of the first rank have given their whole attention to it: hence we may hope that this important question will ere long make striking progress.

My purpose in this essay is to examine carefully one of the most controverted points in the history of the development of the Infusoria—the metamorphosis of the species of the family of Vorticellina into the corresponding species of *Acinetæ*.

Before giving the results of my own observations, I shall endeavour to trace, as concisely as possible, the history of the subject I intend to treat.

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I shall not enter into any detail relative to the description of the Vorticellina and the *Acinetæ*, as this would lead too far away from my subject: I refer my readers to the great work of Ehrenberg, and to other general treatises on the Infusoria: I shall deal with the history only from the point where the question of the metamorphoses arose.

Dr. Pineau, in an essay published in the 'Annales des Sc. Naturelles' (3 sér. iii. p. 182, and iv. p. 103), made known that he had observed the Infusoria described by Ehrenberg under the name of *Acinetæ*, become transformed into *Vorticellæ*. No deep acquaintance with microscopic studies is requisite to convince any one that the observations of Dr. Pineau are deficient in that exactitude which must be demanded of every conscientious naturalist; so that I should not attach any importance to the results he supposed himself to have obtained, had he not been the first who sought to establish a relationship between the *Acinetæ* and the Vorticellina.

A few years later M. Stein published, in Wiegmann's 'Archiv' (1849), his researches upon the developments of Vorticella microstoma, Vaginicola crystallina, and Epistylis nutans. He sought to prove, by these three examples, that Infusoria belonging to the family of the Vorticellina became transformed into Acinetæ. This opinion was adopted pretty generally among the German naturalists, in spite of the important adversaries it met; in the front rank of the latter must be named the celebrated Ehrenberg.

In 1854, M. Stein published a new and very extensive work upon the development of the Infusoria, and he enlarged particularly upon the metamorphoses of the Vorticellinæ.

He endeavoured to show that each species of the family of Vorticellina has a species of *Acineta* corresponding to it; that ciliated embryos originate in the interior of the *Acineta*; and that these ciliated embryos, when set free, become transformed into Vorticellina.

M. Stein gives this last part of his opinion only as an hypothesis, which he considers very probable, but which he has not succeeded in proving, having never been able to trace the ulterior development of the ciliated embryo.

This author believed that he proved the transformation of the Vorticellina into *Acinetæ*, first by a direct observation upon *Vaginicola crystallina*, then by the simultaneous presence in the same infusions of numerous species of Vorticellina and corresponding species of *Acinetæ*, and finally by the alternate appearance of Vorticellina and *Acinetæ* in the same infusion.

Last year appeared a very remarkable essay on the Infusoria, by M. Lachmann*, in which he strongly attacks M. Stein's

* Annals of Natural History, ser. 2. xix. pp. 113, 215.

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opinions on the development of the Vorticellina, and denies the metamorphosis of the latter into *Acinetæ*; he thinks that these two families should remain separate, and that no bond of relationship exists between them.

He attacks M. Stein's opinion by well-grounded and serious objections, and regards as inexact and inconclusive the observation by which M. Stein thought to demonstrate the metamorphosis of Vaginicola crystallina into Acineta mystacina.

With regard to the arguments used by M. Stein, derived from the simultaneous appearance of the *Vorticellæ* and the *Acinetæ*, and the alternation of the appearance of these two Infusoria in one and the same infusion, M. Lachmann objects to them as proving nothing.

In the course of the present paper I shall have occasion to recur to these different objections; for the moment, I shall confine myself to mentioning them.

M. Lachmann finally overturns completely the hypothesis put forward by M. Stein upon the transformation of the ciliated embryos of the *Acinetæ* into *Vorticellæ*; he shows, by numerous examples, that these embryos become transformed into *Acinetæ*; and he attributes the first discovery of this important fact to J. Müller.

The essay of M. Lachmann had not yet reached Belgium, last year, at the time when I presented to the Royal Academy of Sciences the results of my researches upon *Epistylis plicatilis*. The following is the *résumé* of my observations which I gave in that memoir :—

"*Epistylis plicatilis*, before or after it has acquired its full growth, becomes enveloped in a cyst, either remaining attached to its style, or abandoning it, or re-uniting in one and the same cyst.

"Entirely enclosed in the cyst, the animal undergoes a total transformation. Its mouth, peristome, and integuments disappear by dissolving into a sarcodic liquid, in which are suspended globules of different sizes; the nucleus of the *Epistylis* alone appears able to resist this solution. Upon the surface of the sarcodic liquid a new resisting contractile integument makes its appearance, covered with vibratile cilia, and closed at all points.

"The *Epistylis* is then metamorphosed into a new Infusorium having much analogy to the *Opalinæ* which are met with in Frogs.

"The Opalina (we will provisionally apply this name to the new Infusorium originating by the metamorphosis of the Epistylis) revolves, and acquires such dimensions that the cyst, not being elastic, bursts, and gives passage to the animal which it

previously contained. Once free, the latter swims about, and seeks a suitable place on which to fix itself. Having found this, it proceeds to undergo a new metamorphosis, which may produce two different forms. Sometimes the *Opalina*, which is spherical or more or less oval, becomes fixed by one of its extremities, whence arises a style, which grows rapidly; at the other extremity appear four bundles of retractile tentacles.

"In the second case, the *Opalina* does not become fixed by one of its extremities, but seems to become flattened out upon the foreign body; it remains sessile, and a more or less considerable number of bundles of tentacles appear on its circumference. In the two preceding cases, the vibratile cilia covering the integument of the *Opalina* vanish from the moment when it becomes fixed.

"The two forms which I have just described are Acineta. The first is identical with that represented by M. Stein, pl. 1. fig. I. D. of his work; the second is an Acineta not hitherto described. The metamorphoses of Epistylis plicatilis stop here. The Acineta grow, and become more and more developed. In their interior is found a nucleus, which increases in size, and makes its way towards the internal surface of the integuments. By the contractions of the animal, the latter become ruptured, and the nucleus is set free. This nucleus, which is really a bud, of discoidal form, moves with extreme activity by the aid of long vibratile cilia which decorate its surface. The Acineta give birth, successively, to several ciliated buds, and terminate their existence without undergoing any further metamorphosis.

"The ciliated buds, after their emission from the Acineta, become metamorphosed into young Acineta; they affix themselves to a foreign body, either remaining sessile or producing a style; their vibratile cilia disappear, and are replaced by four bundles of tentacles.

"The new nuclei reproduce new ciliated buds in their interior."

From this it will be seen that I thought myself the first discoverer of the transformation of the ciliated embryos into young *Acineta*; I hasten to restore the property in this discovery to its rightful owner, the illustrious physiologist, J. Müller.

Now that I have given the history of the question, I shall attempt, from the materials furnished by the observations of my predecessors and by my own, to show that what I have described of *Epistylis plicatilis* will apply to many species of Vorticellina, and perhaps to all.

I shall examine, then, 1. the encystment; 2. the transformation of the Vorticellian in the interior of the sac into an Infusorium with its whole surface ciliated, and without any orifice in

its integuments (*Opalina* or *Bursaria*); 3. the transformation of the *Opalina* into an *Acineta*; 4. the appearance of ciliated embryos in the interior of the *Acineta*; and, 5. the transformation of the ciliated embryos into young *Acineta*.

1. The Encystment.

The encystment, observed first by M. Stein in different species of Vorticellina, and subsequently by several naturalists in many other Infusoria, now appears to exist among all the animals of this class. I shall deal here only with the Vorticellina. I shall first indicate in what species the encystment has been observed; then, how it takes place; I shall discuss, in the third place, the view which is to be taken of this phænomenon, and what is its probable purpose.

I have observed the encystment in four species of Vorticellæ. First, in Vorticella microstoma: this is the example in which it is most easy to see the phænomenon; for in almost all liquids where it is met with, we find cysts at the same time, which, as we shall see further on, does not always happen with the other species. When an infusion containing Vorticella microstoma is concentrated by evaporation in the open air, the cysts become very numerous. The thickness of the cyst differs in different individuals; sometimes it is thin and fragile, sometimes thick and hard; sometimes it is covered with prominent points. M. Stein was the first to describe the phænomenon of encystment in Vorticella microstoma.

I observed the encystment in a species of Vorticella not hitherto described, and which I shall call Vorticella microstyla, on account of the shortness of the style, which never forms a complete turn of a spiral when the animal contracts. I have met with this species only in a single spot in the environs of Brussels. I hope to give a more complete description of it on a future occasion. As the cysts, in this species, very closely resemble those of Vorticella microstoma, they do not require a particular description.

I have several times met with cysts of *Vorticella Convallaria*; but they are more difficult to observe, because, this species being more delicate than those of which I have just spoken, the individuals mostly die without becoming encysted.

Lastly, I have observed the phænomena of encystment in a fourth species of *Vorticella*. This species, which I met with upon our coast at Ostend, has not yet been described; it is extremely remarkable on account of a membranous prolongation surrounding the peristome, which gives it, when expanded, the form of a parasol; when it is contracted, this membrane becomes plaited and folded up in the interior of the body.

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M. Stein has observed the encystment of Vorticella nebulifera. In the genus Carchesium, I have observed the cysts of three species—those of Carchesium polypinum, of Carchesium ramosissimum, and of Carchesium pygmæum; there is scarcely any difference between them, and they entirely resemble the cysts of the Vorticellæ.

In the genus *Epistylis* I have only been able to observe the encystment in two species—*Epistylis plicatilis*, and an *Epistylis* which I think new, and which I have often met with living parasitically upon the posterior extremity of *Tubifex* and *Nais*. M. Stein also has observed the encystment of *Epistylis plicatilis*. I have sought in vain for the cysts of *Epistylis grandis* and *E. flavicans*, two species very common in our environs; I attribute this to the difficulty of preserving these animals alive in vessels in the study.

In the genus Opercularia, my observations have been made on Opercularia nutans, O. Lichtensteinii (Stein), and O. microstoma. I have seen the encystment only in the first of these three species; the two others being far more rare, it is not surprising that this phænomenon should have escaped me.

Finally, M. Stein has observed and described the encystment of Vaginicola crystallina; I have made a similar observation.

Summing up all these observations, I shall conclude that species susceptible of encystment are met with in all the genera of the family of Vorticellina, and that it is very probable that this phænomenon presents itself in all, when favourable circumstances tend to induce it.

The Vorticellina may become encysted at all periods of their existence; they are encysted either while remaining attached to the style or after they have abandoned it, subsequently to the appearance of a basilar crown of cilia. Lastly, while the Vorticellina are reproduced by fission, they may still become encysted; and I have observed among them all the intermediate conditions between the commencement of the division and its completion, simultaneously with the appearance of cysts.

The encystment takes place in the same manner in all the Vorticellina in which I have observed it. The individual which is about to present this phænomenon contracts slightly, and closes its peristome; around it appears a cloud, formed by a viscid liquid, which is probably the result of a cutaneous secretion. In this liquid are formed granules, which, augmenting more and more in number and adhering together, finally form a membrane, which becomes hard and resisting, although soft and flexible when first produced. The cyst thus formed does not change its state, or augment in thickness by the deposition of new granules in its interior. When a cyst encloses two indi-

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viduals, it is often reniform, sometimes oval; the surface of the cyst becomes in some cases rough with little points.

The cause of the encystment escapes us, like the causes of almost all physiological phænomena. For its explanation we may have recourse to two hypotheses :--either the animal is induced to become encysted by the influence of an internal causethe phænomenon of encystment being then physiological, normal, and occurring necessarily; or the animal becomes encysted from the influence of external agents-the phænomenon then being abnormal and depending on chance. Of these two hypotheses the second appears the more probable; indeed I have always remarked that most of the Vorticellina become encysted. when the liquid containing them evaporates through exposure to the air; moreover, we find a greater number of cysts in winter than in any other season. I conclude from this that drought and cold are two causes of encystment; that these two causes are probably not the only ones, but that there doubtless exist others which it is more difficult to appreciate.

The encystment of the Vorticellina appears to have a double purpose: first, to withdraw these very delicate animals from the destructive action of drought and cold; in the next place, to allow them to undergo certain metamorphoses protected from all external influences.

2. Transformation of the Vorticellian, in the interior of the cyst, into an Infusorium ciliated over the whole surface, and presenting no orifice in its integuments (Opalina or Bursaria).

The observations of M. Stein, M. Lachmann, and myself agree in showing that the majority of the Vorticellina may remain in the interior of the cysts without undergoing metamorphosis; they are then under the influence of a state analogous to the hybernal sleep of the higher animals. When circumstances are favourable, that is to say, when humidity and a certain degree of heat are restored, they burst their envelope and resume their former life.

In M. Stein's work, he treats of several metamorphoses undergone by the Vorticellina in the interior of the cysts; not having observed these, I shall not speak of them, and shall occupy myself solely with that transformation which I have indicated at the head of this section.

The metamorphosis of a Vorticellian, in the interior of a cyst, into an Infusorium ciliated over the whole surface, was for the first time described by me in my memoir on the development of *Epistylis plicatilis*. The following is the account I gave of the phænomenon.

The Epistylis plicatilis, in the interior of the cyst, becomes

attenuated, and seems to fold upon itself; the sarcodic substance traverses its integuments in all parts; from time to time it still contracts; and a complete solution soon affects the whole animal, so that we find in its place merely a homogeneous sarcodic liquid, containing granules, together with the nucleus, which resists the general destruction. In the sarcode there takes place a process which may be in some measure compared with what occurs in the vitellus after the fecundation of an ovum. The granules, becoming united together, form groups which soon divide and subdivide; at the same time an integument is formed upon the surface, in the same manner as the blastoderm appears in the eggs of the inferior animals. This integument is contractile, covered with vibratile cilia, and closed at all points.

The transformation is then complete; the cyst contains a new Infusorium, which may be compared to the *Opalinæ* or *Bursariæ*, which are met with in the intestines of the Batrachians.

This description of *Epistylis plicatilis* may be applied in all its details to the Vorticellina in which I have observed the transformation into an Infusorium ciliated over the whole surface. It will be useless to revert to it. I shall simply indicate the species in which I have observed it. This metamorphosis may be found almost at will in *Epistylis plicatilis*; but it is not so with other species of the same genus. I have sought for it in vain in *Epistylis grandis* and *E. flavicans*; and I have only met with it in the *Epistylis* of *Tubifex*, the new species of which I have already spoken.

In the genus Vorticella, I have observed this metamorphosis in Vorticella microstoma, microstyla, Convallaria, and in the Vorticella with a fringed peristome described above.

Carchesium polypinum and arbuscula likewise undergo similar metamorphoses in the interior of the cysts.

3. Transformation of the Infusorium ciliated all over (Opalina or Bursaria) into an Acineta.

I have said, in the historical part of my essay, that M. Stein was the first who sought to demonstrate the metamorphosis of the Vorticellinæ into Acinetæ; from what I have just said, in the preceding paragraph, it may be seen that my opinion differs entirely from his upon the point—that I do not suppose, with him, the immediate transformation of the Vorticellina into Acinetæ, but that an intermediate metamorphosis exists.

Hence none of the arguments produced by M. Lachmann against M. Stein's opinion can touch mine; I shall, however, endeavour to reply to some of them, because they tend to deny the existence of a metamorphosis. But, before commencing this discussion, I will give the description of this new transformation.

I have indicated in the preceding paragraph that certain Vorticellina become transformed, in the interior of a cyst, into a spherical Infusorium having an integument closed at all points, and entirely covered with vibratile cilia. This new Infusorium performs, within its envelope, a continual rotation. In another paper, I have compared this rotation to that performed by the embryos of Gasteropod Mollusca within the egg.

While the metamorphosed Vorticellian revolves, it undergoes development, increases in size, and its whole surface becomes covered with folds; finally, a moment arrives when the cyst, yielding to the pressure exerted in its interior, bursts; the ciliated Infusorium becomes free, and swims with a rotating movement.

To discover how this Infusorium becomes transformed into an *Acineta* requires attentive observation, in order to avoid all the chances of error which may present themselves, and which are numerous.

I believe myself authorized in supposing the existence of this metamorphosis, because I have observed Infusoria which presented, on the one hand, all the characters of *Acineta*, and, on the other, the characters of the Infusorium produced by the transformation of the Vorticellina.

Three times I have observed individuals of Acineta mystacina already provided with tentacles, and which had the spherical form and the body covered with vibratile cilia. I have doubtless seized in those cases the moment of the metamorphosis of the ciliated Infusorium (Opalina) into an Acineta. It may be objected that the cilia with which these Acineta were covered belonged to the embryonary state; the answer to this objection is easy: the cilia of the embryos are arranged in a totally different manner, and occur only upon Acineta of very small size; they fall off very early, before the appearance of the tentacles.

I shall now discuss the objections of M. Lachmann against the theory of M. Stein, so far as they might be applied to my opinion. M. Lachmann thinks that the forms indicated by M. Stein as degrees of transition between the Vorticellina and the *Acinetæ*, are really only different species of Infusoria, which have no other relation beyond a more or less considerable resemblance. This objection is indeed applicable to the observations of M. Stein. That author has not taken sufficient pains to show the interconnexion of the different transitory forms. For my own part, I think I am entirely out of reach of this objection, and what is said above sufficiently proves it; thus I have demonstrated how certain Vorticellina become transformed into ciliated Infusoria

(Opalina), and how these Opalinæ become covered with tentacles and metamorphosed into Acinetæ.

The second objection of M. Lachmann against M. Stein rests on the opinion that the simultaneous appearance of *Acinetæ* and Vorticellina in the same infusion cannot be regarded as a sign of relationship between these two species. I quite agree with M. Lachmann upon this point; however, I believe that the simultaneous appearance of two Infusoria always and everywhere in the same infusion affords great probability of the real existence of the metamorphosis of one species into the other. Numerous observations have led me to the certainty that one may almost affirm, *à priori*, that where a species of Vorticellina is observed, we shall find a species of *Acineta*, and vice versa.

Not only have I found most of the *Acinetæ* described by M. Stein as accompanying certain Vorticellina, but, further, when I have met with a new Vorticellian, I have at the same time found a new species of *Acineta*.

A third objection of M. Lachmann must be taken into serious consideration. According to him, the alternation of the appearance of the Vorticellina and the *Acineta* in the same infusion does not in any way indicate that one species arises out of the transformation of the other. Indeed this alternation occurs with a very great number of Infusoria; and, as M. Lachmann has rightly said, this is what led MM. Pineau, Gros, and Laurent to suppose that most of the species of Infusoria are only stages of development of one and the same species. M. Lachmann adds—"An alternation of the appearance of certain Infusoria may really give a demonstration of the relationships which exist between them, if one makes certain, by complete isolation in a very circumscribed space, that only individuals of one species exist there."

M. Stein has, it is true, neglected this experiment; for my own part, I have repeated it several times, and, after numerous efforts, I have discovered *Acinetæ* in the liquid in which I had isolated specimens of *Epistylis plicatilis*. I must confess, however, that I do not attach the same importance to these experiments that M. Lachmann attributes to them; the causes of error are too numerous,—above all, on account of the great difficulty of completely isolating a species of Infusorium.

The other objections of M. Lachmann are addressed to the second portion of M. Stein's theory, that is to say, to the transformation of the embryos of *Acinetæ* into Vorticellina. It is unnecessary for me to discuss this here; that question is now cleared up, as I have already said, in the historical summary which stands at the head of this paper.

M. Lachmann terminates his objections by saying that the

metamorphosis of Vorticellina into *Acinetæ* is improbable, because it cannot be compared with anything taking place in other animals. I shall answer this in the words of a great physiologist: "One must be very bold to assign limits to nature."

4. Appearance of Ciliated Embryos in the interior of the Acinetæ.

The discovery of the origin of ciliated embryos in the interior of the Acinetæ is due to M. Stein. M. Lachmann announces that he has made a similar discovery in a great number of Aci-I also found this embryo in the Acineta of Epistylis netæ. plicatilis, and subsequently in all the Acinetæ I have met with, among which are many species not yet described. All naturalists are now agreed as to the appearance of the ciliated embryos in the Acineta, and their formation at the expense of the nucleus; but one point is still controverted, namely the manner in which the nucleus behaves during the production of the embryo. According to M. Stein, the division of the nucleus appears to precede the formation of the embryo; but M. Cohn regards this division as improbable. It appears that M. Lachmann has studied this question with much care; but as he only gives the result of his observations on the Infusoria in general, and not especially for the Acinetæ, it is impossible to know his opinion upon this point. With regard to myself, notwithstanding all the pains I have taken. I have never been able to see the division of the nucleus of the Acinetæ before the production of the embryo, as indicated by M. Stein; on the contrary, I have always seen the nucleus totally converted into an embryo, and after the expulsion of the latter, a new nucleus has been formed, which, in its turn, became transformed into a new embryo, and so on.

5. Transformation of the Ciliated Embryos into young Acinetæ.

M. Stein, after discovering the production of ciliated embryos in the interior of the *Acinetæ*, stated, as a very probable hypothesis, that these embryos, once free, become transformed into Vorticellina; however, he never succeeded in tracing the ulterior development of these embryos; the latter always escaped him. More fortunate than M. Stein, M. J. Müller succeeded in tracing these embryos, and saw them become fixed, and transformed into young *Acinetæ*. M. Lachmann arrived at the same result.

These observations of MM. Müller and Lachmann were not yet known, as I have already said, in Belgium when I presented to the Academy my work on the development of *Epistylis plicatilis*; in that work I described this curious transformation of the ciliated embryo into a young *Acineta*, thinking myself the first to observe it. Since then, I have succeeded in detecting this metamorphosis in almost all the embryos. Does this transformation of the ciliated embryo into a young Acineta always take place? It is allowable to doubt this; twice I have seen ciliated embryos become enclosed in a cyst, instead of changing into young Acinetæ. I was unable to carry the observation further, and ascertain whether or not the Infusorium underwent new transformations in the interior of the cyst. Further researches are required to clear up this obscure question.

II.—On the Development of the Vegetable Ovule called 'Anatropous.' By JOHN MIERS, F.R.S., F.L.S., &c.

ALTHOUGH the changes that take place in the development of the vegetable ovule have long since occupied the attention of the ablest physiological botanists, it is evident that the real nature of its mode of growth is not yet well understood. My first object therefore is to show that the doctrine upon this important subject, as taught in the best elementary works, is founded upon a very grave error. I was led into this inquiry by my desire to ascertain the nature of the fleshy covering enveloping the hard tunic in certain seeds *, and which appeared to me arilloid in its nature. This was contested by Dr. Asa Gray, who considered these two very opposite kinds of tunics as one baccate testa, both deriving a common origin from the primine of the ovule[†]. To this view I was unwilling to subscribe; and in my subsequent discussion of the subject, trusting fully to the orthodoxy of the common creed of botanists on the development of the ovule, I argued t that the fleshy covering in question must be an expansion or growth of the placentary sheath, because it enclosed the raphe : and so it is undoubtedly-but not in the light of an extraneous expansion, as I then viewed the question. This induced me to examine, by personal observation, the actual progress of growth of the ovule in certain plants which produce what have been called anatropal seeds; and I soon became convinced that I had been led into an error of inference, solely by my faith in the universally prevalent Having lately completed the investigation of many creed. Rhamnaceous and Anacardiaceous seeds, in which several novel points of structure have been observed, which are difficult to explain, I am desirous, before the publication of these results, that the real nature of the development of the ovule should be well understood. I therefore now proceed to show that the doctrine upon this subject, as at present taught, is completely fallacious.

* Trans. Linn. Soc. xxii. 81.

† Journ. Linn. Soc. ii. 106.

‡ Ann. Nat. Hist. 3rd ser. i. 276.